THE PTEROBRANCH *RHABDOPLEURA* IN THE ENGLISH EOCENE

BY

HENRY DIGHTON THOMAS

AND

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WITH AN APPENDIX ON

THE LONDON CLAY AT LOWER SWANWICK HAMPSHIRE

BY ARTHUR WRIGLEY

Pp. 1–24; *Pls.* 1–3; 4 *Text-figures*

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THE PTEROBRANCH *RHABDOPLEURA* IN THE ENGLISH EOCENE

By HENRY DIGHTON THOMAS *and* ARTHUR GEORGE DAVIS

(*With Plates* 1–3)

SYNOPSIS

A species of *Rhabdopleura*, the first pterobranch to be found fossil, is described from the London Clay of Hampshire. It helps to bridge the gap between the modern representatives of the group and the last dendroid graptolites in the Carboniferous, for which there is strong evidence that they were at least very closely allied to the Pterobranchia.

I. INTRODUCTION

EARLY in 1930 one of us (A. G. D.) brought to the Museum a pebble from the London Clay of Lower Swanwick, Hampshire, on which was a small, encrusting organism. Its identification as a species of *Rhabdopleura*, unknown until then as a fossil, was confirmed by the other author, and it was exhibited as such at a Conversazione of the Staff Association of the Museum on 5 March 1930. For various reasons, including the search at infrequent intervals for additional well-preserved specimens, and, later, the recent war, the description of this remarkable fossil has had to be delayed.

We are indebted to Mr. A. Wrigley for the Appendix on the stratigraphy of the clay-pit at Lower Swanwick; to Dr. Anna B. Hastings and Dr. E. Trewavas for access to Recent material of *Rhabdopleura* in the Museum; to Miss E. C. Humphreys and Mr. J. V. Brown, respectively, for the drawings and photographs illustrating this paper; to the Council of the Palaeontographical Society of London for permission to reproduce Text-fig. 1; and particularly to Dr. Hastings for invaluable discussions on the genus and for her helpful criticisms of the typescript. One of us (A. G. D.) also wishes to acknowledge a Royal Society Government Grant for the field collecting in the course of which the fossils were discovered.

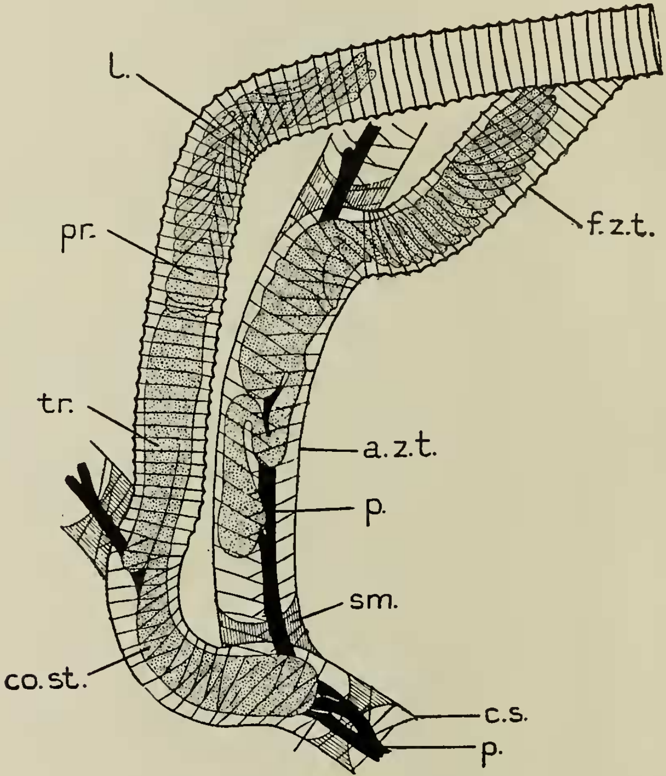
II. THE COENOECIUM OF *RHABDOPLEURA*

(TEXT-FIG. 1)

The following account is mainly based on Lankester (1884), Schepotieff (1907 *a, b*), and van der Horst (1936).

Recent species of *Rhabdopleura* are colonial animals which secrete around themselves a series of transparent, chitinous tubes forming the *coenoecium*. The tubes are analogous to those of worm-tubes and do not form an exoskeleton comparable to that, for instance, of the crustacea.

From the point of origin of the colony a bud develops (sometimes there are two developing in divergent directions). The parent bud (immature zooid) moves forwards at the end of a growing soft stalk, *gymnocaulus*, and secretes around itself that part of the tubular coenoecium known as the *creeping stem*, which is cemented by its basal wall to the surface of such underlying foreign bodies as pebbles, corals, ascidians, and shells. The growth-rings of this creeping stem consist of alternating segments which run obliquely backwards from the sides and meet in a zigzag ridge usually along or near the middle of the upper surface—although Norman (1921: 99, fig. 3) shows the zigzag sutures at the sides in *R. annulata* Norman, our observations



TEXT-FIG. 1. *Rhabdopleura normani* Allman.
Two zooidal tubes with retracted, sterile zooids, and part of a creeping stem. ×29.
a.z.t., adherent part of zooidal tube; *c.s.*, creeping stem; *co.st.*, contractile stalk; *f.z.t.*, free part of zooidal tube; *l.*, lophophore; *p.*, pectocaulus; *pr.*, proboscis; *sm.*, septum; *tr.*, trunk. (After Bulman, 1945, and Schepotieff, 1907*a*.)

do not confirm this. The sutures between adjacent bands stand up as oblique ridges. Behind the advancing immature zooid other buds develop from the gymnocaulus to which they remain attached by short branches. Each of these gradually becomes mature, and when it attains a certain size a transverse septum is formed on its distal side across the creeping stem which separates it from the next distal bud, but which is pierced by the gymnocaulus. At a certain stage this young zooid breaks through the wall, usually the upper wall, of the creeping stem and builds its own living tube, the *zooidal tube*, in continuity with it. The zooid remains attached to the original gymnocaulus—the attachment is the *contractile stalk*, by which the zooid can withdraw well within its tube.

The *zooidal tube* may be upgrowing and not adherent to a foreign body (i.e. free), or it may have a proximal adherent part of a greater or less length in addition to a distal free part. It is because the zooidal tubes are not always wholly free that we introduce that term as preferable to 'free living tubes': there are obvious objections also to 'peristome'. The adherent part of a zooidal tube comes off from the side of the creeping stem and shows similar suturing to it, although, in the fossil species at any rate, the sutures are more closely arranged. The free part, however, is made up of narrow, annular growth-rings: these are separated from one another by prominent circular ridges (sutures), and each is interrupted by an oblique suture marking the junction of its first- and last-formed parts. The terminal immature zooid at the distal end of the gymnocaulus also ultimately becomes mature and forms a vertical, free, zooidal tube—further extension of the creeping stem is then impossible.

The gymnocaulus is free, and it remains so for some distance behind the advancing bud in the creeping stem. But with development it becomes pigmented and chitinized, and forms the *pectocaulus*, the organ which is peculiar to *Rhabdopleura* and which distinguishes it from all other living animals. This term of Lankester's (1884: 635) is better than 'stolon' ('schwarze Stolo' of Schepotieff), for stolons of a different nature are known in other phyla: 'stolon' is best used as a general, descriptive word. The pectocaulus shows as a dark, narrow, cylindrical, rod-like stolon through the transparent chitinous material of the creeping stem. It is composed of an outer and inner cell-layer and is surrounded by a resistant chitinous sheath: its lumen may become filled with a chitinous axial rod. Distally the pectocaulus is free, but with progressive chitinization it first comes to rest against the basal wall of the creeping stem and then becomes adherent to it and finally embedded in it. The proximal end of the contractile stalk of each zooid is also chitinized for a short distance so that short side branches of the pectocaulus exist; indeed, these branches of the pectocaulus may extend along the whole length of the adherent parts of the zooidal tubes (Lankester, 1884: 625, pl. 37 *bis*, figs. 1, 2). Further, the gymnocaulus (and therefore the pectocaulus) may fork, each part giving rise to a series of zooids.

III. *RHABDOPLEURA EOCENICA* Thomas & Davis

PHYLUM CHORDATA

SUB-PHYLUM HEMICHORDA

Class *PTEROBRANCHIA*

Genus Rhabdopleura Allman

Type species (by monotypy): *R. normani* Allman, 1869 *a*: 311; 1869 *b*: 439; 1869 *c*: 58, pl. 8. Recent, Shetland seas at 90 fathoms.

Rhabdopleura eocenica Thomas & Davis

Pls. 1–3; Text-figs. 2–4

1949 *Rhabdopleura eocenica* Thomas & Davis, p. 79

Material and Horizon. Several specimens, mostly fragmentary, preserved in iron pyrites and encrusting flint pebbles at the base of Bed C of the London Clay, Yprésian, Bursledon Brick Company's clay-pit, Lower Swanwick, $\frac{5}{8}$-mile ENE. of Bursledon railway station, Hampshire (full National Grid Reference 41/500099)—see Appendix, p. 14.

HOLOTYPE. H.4170a (Pl. 3, fig. 1).

PARATYPES. H.4168–H.4187 (excluding H.4170a) and Geol. Surv. Mus. 83867—most numbers include several specimens.

DIAGNOSIS. *Rhabdopleura* with a creeping stem about 150–195 μ in diameter and growth-rings 60–72 μ wide; zooidal tubes recumbent and adherent proximally but free distally, the adherent parts 150–175 μ in diameter and their growth-rings 40–55 μ wide, the free parts up to 175 μ in diameter and with growth-rings 40–45 μ wide; pectocaulus about 22 μ in diameter.

NOTE ON MEASUREMENTS. Throughout this paper the width of the growth-rings of *R. eocenica*, i.e. the distance apart of the sutures, was measured at *right angles* to the sutures and not in the linear direction of the tubes. That measurement not only gives the true width of the growth-rings, but, in the fossils, is also more accurately made.

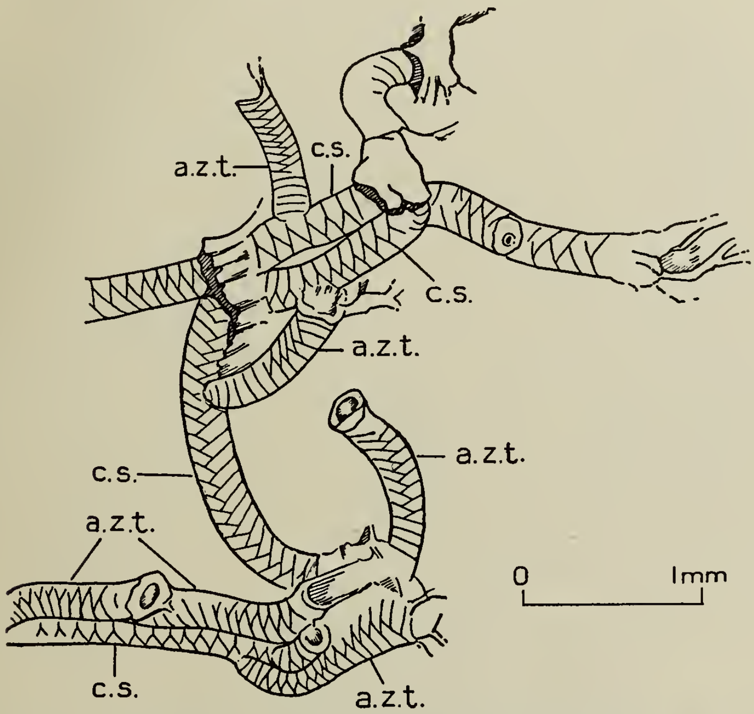
DESCRIPTION:

Coenoecium. The coenoecium is small, the longest piece preserved reaching about 3·5 mm. in length. It is not always possible to follow any one coenoecium far, because the preservation is such that one cannot always be certain whether it has branched or whether it has crossed, or been crossed by, another one. In any case the coenoecia have been broken or worn so that only relatively short lengths are found on the pebbles.

Creeping Stem. The creeping stems are not straight, but may curve extensively. Their basal walls are firmly adherent to the pebbles they encrust. In cross-section these tubes may be approximately semicircular, or they may be sub-triangular, when the sides are flat or nearly so and slope away from the rounded, median upper edge. The sutures are of the type normal in *Rhabdopleura* and meet to give the characteristic median zigzag line on the upper surface. Their distance apart averages between 60 and 72 μ. They are prominent, but the preservation prevents any accurate measurements of the degree to which they project beyond the general width of the tube. Thus the measurements of the width, which varies between 150 and 195 μ, are inclusive of the sutures. Bifurcation of the creeping stems (as distinct from the development of the adherent parts of zooidal tubes) occurs, e.g. in H.4168b and probably in H.4169.

Zooidal Tubes. These develop from the sides of the creeping stems. There is no regularity in their spacing and they are not confined to one side. For example, in H.4169 (Pl. 1; Pl. 2, fig. 1; and Text-fig. 2) four consecutive zooidal tubes come off from a creeping stem at intervals of approximately 630 μ, 412 μ, and 220 μ, respectively, and the later two are developed from the side opposite to that of the first pair.

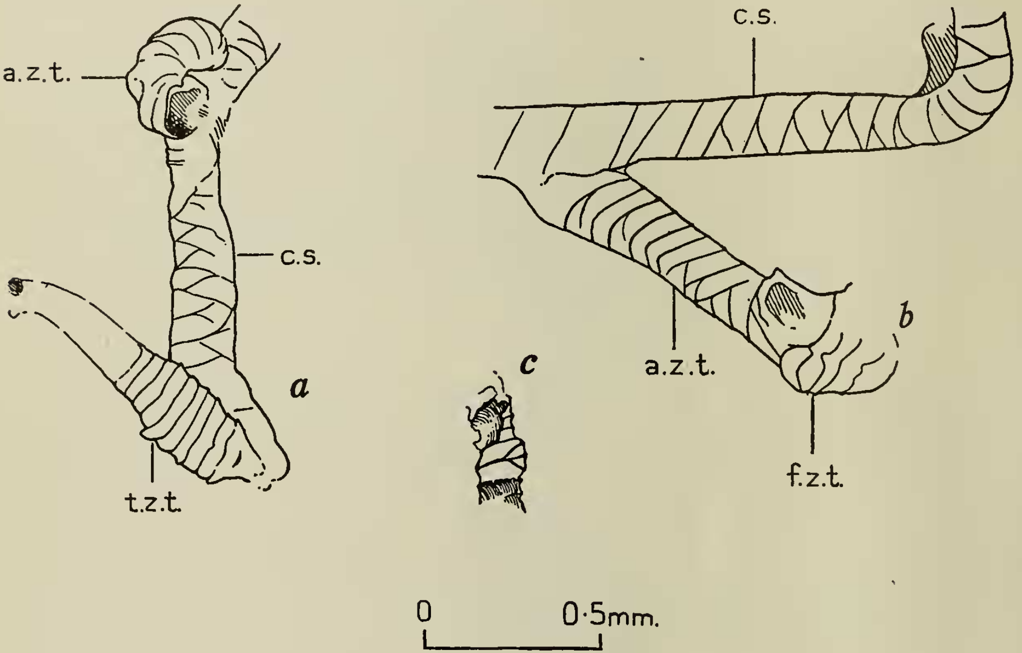
The zooidal tubes consist of a proximal adherent part and a distal free part. The adherent parts appear usually as relatively short side-branches, between 0·74 and 1·2 mm. long—the length of the complete one which retains part of its free tube (H.4168b) is approximately 0·87 mm. They are generally slightly curved, but they may be much bent and even folded back against themselves. They may lie alongside the creeping stem or at any angle with it up to nearly a right angle, but the initial growth is always partly forwards. They resemble the main creeping stem in appearance because the suturing is similar, but they tend to be more rounded and do not reach the same width (only 150–175 μ), while the sutures are less widely spaced



Text-fig. 2. *Rhabdopleura eocenica* Thomas & Davis
A series of intersecting coenoecia, H.4169. (See Pl. 1 and Pl. 2, fig. 1.)
a.z.t., adherent part of zooidal tube; *c.s.*, creeping stem.

(40–55 μ). The first few sutures (usually three or four), however, where the proximal end swells out of the side of the creeping stem, do not seem to have the alternating, zigzag arrangement, but appear instead to be ring-like (Text-figs. 2, 4). The distal ends of the adherent parts of the tubes are sometimes seen to be slightly turned upwards when they are also somewhat crushed (Pl. 1 and Pl. 2, fig. 1): these are the places where the vertical free parts of the zooidal tubes commenced.

The free parts of the zooidal tubes which are preserved are fragments. They include one terminal tube in contact with the creeping stem (H.4168a—Pl. 3, fig. 4, and Text-fig. 3 *a*), several free tubes in contact with their proximal adherent parts (e.g. H. 4170a—Pl. 3, fig. 1; and H.4168b—Pl. 3, fig. 2, and Text-fig. 3 *b*), and some isolated specimens (e.g. H.4171a—Pl. 2, fig. 2). They are generally much flattened and incomplete, and have similar characters. The preserved part of the terminal tube is 500 μ long, but there are indications on the pebble that it was probably at least as long again. The longest free part of a zooidal tube preserved is 3·9 mm. (H.4171a—Pl. 2, fig. 2). The greatest width of a flattened tube is 228 μ, and of a tube which is only slightly crushed 174 μ. The growth-rings are circular and their average width (40–45 μ) is more constant than in the adherent parts of the zooidal tubes.

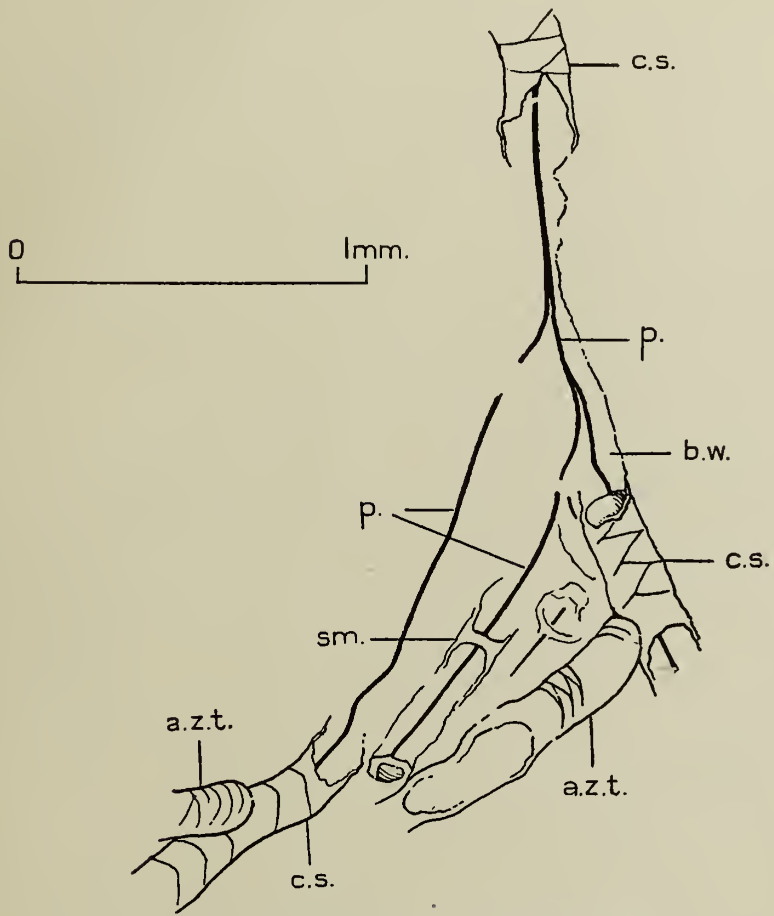


TEXT-FIG. 3. *Rhabdopleura eocenica* Thomas & Davis
3 *a*. A creeping stem with an adherent part of a zooidal tube and a portion of the terminal zooidal tube (note its probable continuation), H.4168a. (See Pl. 3, fig. 4.)
3 *b*. Specimen retaining the adherent and free parts of a zooidal tube in contact with one another and with the parent creeping stem, H.4168b. (See Pl. 3, fig. 2.)
3 *c*. A free part of a zooidal tube showing oblique sutures, H.4170c. (See Pl. 3, fig. 3.)
a.z.t., adherent part of zooidal tube; *c.s.*, creeping stem; *f.z.t.*, free part of zooidal tube; *t.z.t.*, terminal zooidal tube.
[*The scale applies to all the figures.*]

Ten were counted in 412 μ of the terminal tube, while 28 consecutive growth-rings, some distorted, were counted in about 1·325 mm. of the free part of a zooidal tube in H.4171a. The sutures are well-marked, sharp, straight ridges, but the extent to which they project could not be determined. Occasionally the oblique suture which interrupts each ring and which marks the junction of its first- and last-formed parts is clearly seen (e.g. H.4170c—Pl. 3, fig. 3, and Text-fig. 3 *c*; and H.4171a—Pl. 2, fig. 2).

Pectocaulus. The pectocaulus is preserved in iron pyrites as a slender rod which has been revealed by weathering of the rest of the coenoecium. In a few instances it shows in a break in the creeping stem (H.4170b—Pl. 2, fig. 4, and Text-fig. 4);

in others it is seen running along the basal wall from which the sides and upper surface of the creeping stem have been worn away; yet again, e.g. H.4171b (Pl. 2, fig. 3), there are instances where only the pectocaulus is preserved on the pebbles.



TEXT-FIG. 4. *Rhabdopleura eocenica* Thomas & Davis
Specimen showing branching of the pectocaulus and its relation to the creeping stems, H.4170b.
(See Pl. 2, fig. 4.)

a.z.t., adherent part of zooidal tube; *b.w.*, basal wall of creeping stem; *c.s.*, creeping stem; *p.*, pectocaulus; *sm.*, possible part of a septum. [The tubes in the lower part of the figure were mainly destroyed by decomposition of the iron pyrites after the drawing was made but before they were photographed.]

In a few cases, e.g. H.4170b, the pectocaulus is seen to divide into two (or more) long branches, corresponding to branches of the creeping stem. But there are no indications of short side-branches, so that it seems probable that the adherent parts of the zooidal tubes were without a pectocaulus. The width of the pectocaulus is about 22 μ.

Septum. In H.4170b the pectocaulus traversing the basal wall of a broken creeping stem is interrupted by, and seems to pierce, what appears to be the remains of a vertical wall-like structure within the creeping stem (Pl. 2, fig. 4, and Text-fig. 4). This may be a fragment of a septum though we cannot be certain of this.

REMARKS. It is remarkable that these Eocene specimens of *Rhabdopleura* preserve portions of all the main parts of the coenoecium with the possible exception of the septa, although even one of those may be represented. The external characters of the creeping stem and of the zooidal tubes would alone have sufficed to prove the reference to the genus, but the presence of the pectocaulus is conclusive.

The sutures of the creeping stems and of the adherent portions of the zooidal tubes are generally extraordinarily clear in *R. eocenica*, and are much more easily seen than is usual in Recent specimens. This is almost certainly due to the preservation of the fossils in iron pyrites.

The nature of the relatively short tubes which appear as side-branches of the creeping stems was not obvious at first. The absence of breaks in the upper walls of the latter suggested that the zooidal tubes did not consist only of free, vertical elements which rose directly from them. Instead, it seemed probable that the side tubes represent proximal adherent parts from which the free sections of the tubes developed. As the sutures of the side tubes appeared to be closer together than in the main creeping stems, micrometer measurements were made, and these showed that their distance apart varied between 40 and 55 μ, compared with between 60 and 72 μ for the creeping stems. These results indicated a difference in nature between the two structures, and pointed to the short side-branches being adherent parts of zooidal tubes. This was supported by the upturning and crushing of the distal ends of some of these branches (Pl. 1 and Pl. 2, fig. 1), as though they passed into the upstanding, free parts of the zooidal tubes. Complete confirmation of this was given by the discovery of specimens H.4168b (Pl. 3, fig. 2, and Text-fig. 3 *b*) and H.4170a (Pl. 3, fig. 1), for parts of the free zooidal tubes, with some of their circular growth-rings, are preserved in contact with the adherent parts—the latter show the characteristic, relatively close suturing, and can be seen to spring from creeping stems with the more widely spaced sutures. In H.4170a there are the free parts of at least 10 zooidal tubes, which probably belong to two converging coenoecia.

The crushing of the fragments of the free parts of the zooidal tubes is in striking contrast to the uncrushed condition of the adherent parts of the coenoecia and reflects their vertical growth and more delicate structure. The relative rarity of these free tubes among the fossils is also due to their upgrowing form, for they must have been very liable to damage and destruction, especially after the death of the colony. In the Recent species the free parts of the zooidal tubes also show a similar, rather delicate structure and susceptibility to damage.

IV. COMPARISON WITH OTHER SPECIES OF *RHABDOPLEURA*

Seven Recent species of *Rhabdopleura* have been described, namely, *R. normani* Allman (1869 *a*: 311; 1869 *b*: 439; 1869 *c*: 58, pl. 8); *R. mirabilis* Sars (1872: 1, pls. 1, 2; 1874: 23, pl. 1); *R. compacta* Hincks (1880: 581, pl. 72, figs. 8, 8 *a*, 9); *R. grimaldii* Jullien (1890: 180, text-fig. on p. 181; 1903: 23, pl. 1, figs. 1 *a*, 1 *b*); *R. manubialis* Jullien (1903: 24, pl. 1, fig. 2); *R. striata* Schepotieff (1909: 430, pl. 7, figs. 1–16); and *R. annulata* Norman (1921: 98, text-figs. 3–6). Their characters were summarized by Norman (1921: 96).

The validity of these species is, however, doubtful, for the estimation of what are differentiating characters is a matter of some difficulty. The first five are all Atlantic species. Lankester (1884: 626) interpreted Sars's species as synonymous with Allman's, while later Schepotieff (1907 *a*: 470–471) considered that the five Atlantic species were all one. Broch (1927: 468), van der Horst (1928: 14), and Bergersen & Broch (1932: 16) all agreed that there is probably only one living species, although Norman (1921: 96) considered there were six species at least. Johnston (1937: 6) has accepted the validity of *R. annulata* Norman, but has pointed out 'that peristomes [i.e. free zooidal tubes] of the Tasmanian *R. annulata* when mounted in lactophenol under a cover glass changed their form under the light pressure, losing their markedly serrated margin and becoming very similar to *R. normani*'. Later, however, van der Horst (1936: 535, 586–587), tentatively followed by Dawydoff (1948: 487), recognized three species, namely, *R. normani* Allman, which includes all the Atlantic forms, *R. striata* Schepotieff from Ceylon, and *R. annulata* Norman from Three Kings Islands (New Zealand), Celebes, and Tasmania. We accept this grouping.

R. normani is a very variable species, especially in the characters of the zooidal tubes—sometimes there is no adherent portion, while in other instances it is well developed (e.g. Lankester, 1884: 625–627, pl. 37 *bis*). In its general characters *R. eocenica* is closely allied to *R. normani*, especially to those forms in which there is an adherent part of the zooidal tubes without a pectocaulus, e.g. that described as *R. grimaldii* by Jullien. The fossil species, however, has a narrower creeping stem with more closely arranged sutures, wider growth-rings in the free zooidal tubes, and a more slender pectocaulus.

No specimens of *R. annulata* have been described so far with an adherent portion of the zooidal tubes. The free zooidal tubes appear to be somewhat wider in that species (even in the small Tasmanian form—see Johnston, 1937: 6) than in *R. eocenica*, but the width of their growth-rings is about the same; it is doubtful, however, if the projection of the sutures between the growth-rings in the latter is as great as in Norman's species. The creeping stem in the fossil is narrower also, but the pectocaulus is of the same size as in Johnston's specimens but narrower than in Norman's material (1921: 99), which suggests that the diameter of the creeping stem in any species may vary with the diameter of the pectocaulus.

Although it was not possible to obtain any accurate measurements of the thickness of its walls, they are much thinner in *R. eocenica* than in *R. striata*, while the growth-rings of the free zooidal tubes of the latter are very much wider.

V. ECOLOGY OF *R. EOCENICA*

The genus is widely distributed at the present day, ranging from West Greenland in the north and west to the Antarctic in the south and Three Kings Islands (New Zealand) in the east. It is found living at depths varying from 2 to 550 m. It almost always encrusts some foreign body, e.g. pebbles, corals, ascidians, shells, although the form described as *R. mirabilis* Sars was attached to mud and sand particles and associated foraminiferal tests and shell fragments.

All the specimens of *R. eocenica* known show a similar habitat to that of Recent species of the genus in that they lived adherent to pebbles. The colonies occur mainly on one surface, but they are sometimes present on another also. Traces of the fossil are found on probably 1 per cent. of the pebbles, but good specimens are the exception. The pebbles in the bed yielding the *Rhabdopleura* range from ½-in. to about 9 in. in length, but the smaller and larger pebbles do not seem to have been selected by the colonies as habitats: instead they preferred the medium-sized pebbles, 2 in. to 4 in. in length.

A pebble encrusted with *R. eocenica* frequently shows other adherent organisms, notably:

(i) MOLLUSCA. Oysters of a flat and almost nondescript type are common in all stages of growth. They frequently smother colonies of *R. eocenica*. In these cases the lower valve may often be prised off to reveal the hemichordate. The valves are frequently infilled with iron pyrites.

(ii) POLYZOA. Good healthy growths are found on the pebbles; they frequently grow over a neighbouring *Rhabdopleura* coenoecium. The polyzoa are preserved as casts of the interiors, so that determination of the species is very difficult, only *Dittosaria wetherelli* Busk being specifically recognized. Other forms include *Adeonella* sp., a cribrimorph like *Pliophloea*, and *Aechmella* sp.

(iii) ANNELIDA. *Serpula* sp., as pyritic casts of the interiors of the tubes.

(iv) ANTHOZOA. *Paracyathus* sp., as pyritic casts.

(v) FORAMINIFERA. *Webbina* sp., replaced by pyrites.

This fauna associated with *R. eocenica* is similar to that described for the Recent species. It will be noticed that all of these have lost their calcareous parts with the exception of the calcite shell of *Ostrea*. The only forms truly replaced by the iron pyrites are *Rhabdopleura* and *Webbina*. It is obvious that the pyritization of the chitinous tubes must have occurred soon after the death of the animals for so much of the finer details of the coenoecia to be so well preserved.

VI. THE HEMICHORDA AS FOSSILS

No fossil representative of the class Pterobranchia of the sub-phylum Hemichorda, to which *Rhabdopleura* belongs, has hitherto been described; some authors have even doubted the likelihood of their being found as fossils. In contrast, Kozlowski (1947: 107), then unaware of our discovery, has expressed his expectation that pterobranchs would be found preserved in Mesozoic and Tertiary rocks.[1] He has also recorded (1938: 186, 193; 1947: 106) an undescribed genus of the Cephalodiscoidea from the Polish Tremadocian. The present record is, therefore, important in carrying back the geological history of the Pterobranchia, and indeed of the sub-phylum, a considerable distance. The state of development of *R. eocenica* suggests that *Rhabdopleura* has had an even longer history.

Reference must be made to the graptolites, which have generally been placed in the Coelenterata, although other views on their systematic position have been held

[1] While this paper was in the press, Kozlowski (1949: 1505) recorded a species of *Rhabdopleura* from the Danian of Poland.

by various authors. Recent work, however, has shown that they are almost certainly closely allied to the Pterobranchia. Nearly forty-five years ago, Schepotieff (1905) claimed that the graptolites belong to the same class as *Rhabdopleura*, but, as he completely misinterpreted the structure and development of *Monograptus* on which he based his ideas, his hypothesis was not accepted [e.g. Bergersen & Broch (1932: 30), Decker (1947: 130), and Ruedemann (1947: 46–51, especially 50–51), among recent authors, hold very different views]. In 1938, however, Kozlowski published a preliminary note of his observations on certain Tremadocian dendroid graptolites of Poland, in which he recognized the presence of a system of stolons. He amplified this later (1947: 96–107 particularly), while Bulman (1942; 1945: 11–15) confirmed his observations by recording a similar system in a Caradocian species of *Coremagraptus* as well as in other species (1945: 4–5, 7). Kozlowski showed that this system of stolons is identical in its structure and biological role with the gymnocaulus and pectocaulus of *Rhabdopleura*. When this is taken into account with other similarities between the graptolites and *Rhabdopleura* (e.g. the structure of the graptolite rhabdosome and the coenoecium of *Rhabdopleura*, and the mode of budding of the zooidal tubes of the latter and the development of the first theca of the graptolites), Kozlowski's claim becomes very convincing that there is a close genetic relationship between them, and that the class, Graptolithina, to which the graptolites belong, is very closely related to the Pterobranchia. If this be accepted, then *R. eocenica* takes on an increased importance, as it helps partly to bridge the gap between the last dendroid graptolite in the Carboniferous and the Pterobranchia of modern seas.

APPENDIX

THE LONDON CLAY AT LOWER SWANWICK, HAMPSHIRE

By ARTHUR WRIGLEY

Between 1927 and 1932, when the following observations were made, the London Clay was actively excavated at the Bursledon Brick Company's works at Lower Swanwick, Hampshire, half a mile east of Bursledon tollbridge. The section was cut in a hill-side, facing the Hamble river, between the 50 and 100 foot O.D. contours, the base of the working being below the natural level of the site. The strata rise from south to north, the youngest being found only at the top of the southern excavation and the oldest seen only at the base of the northern end.

SECTION (*in descending order*)

Lower Bagshot Sands (14 ft.):

Brown, sandy loams, somewhat bedded, with much dispersed limonite 8 to 9 ft.

Weathering plane

Light grey sands . . . . 4 ft.

D. Flint pebbles, up to 6 in. long, in grey, loamy sand, with numerous decayed fish-teeth . . . . $1\frac{1}{2}$ ft.

London Clay (53 ft.):

C. Grey, sandy clay, weathering brown where it reaches the surface and becoming more clayey below: no fossils seen	25 ft.
Impersistent line of flint pebbles with *Rhabdopleura*	
B. Grey, sandy clay with four lines of septaria	13 ft.
Large septaria, 6 ft. down, have abundant *Turritella*, *Cyprina*, and *Pholadomya* spp.	
A. Grey, sandy clay with numerous fossils	15 ft.
Panopea and *Pitaria* are common at the top. Above a line of tabular septaria, $8\frac{1}{2}$ ft. down, the clay is crowded with very large *Pinna*, *Ostrea*, and *Ficus smithii* (J. de C. Sby.), with a varied molluscan fauna. A rich assemblage of Polyzoa was found upon the large *Ostrea*.	
Bed of black flint pebbles in sandy clay: no fossils seen . . .	4 in.

The bed of flint pebbles, D, taken to be at the base of the Lower Bagshot Sands, yielded a great number of fish-teeth in a most peculiar state of decay which has never been observed in the London Clay. The enamel, which is usually perfect and glistening, was greatly discoloured and corroded, while the roots had become rotten and carious. The species, determined by Dr. E. I. White, are:

Myliobatis 2 species	*Phyllodus* sp.
Lamna verticalis (Ag.)	? *Galeus* sp.
L. vincenti (Winkler)	*Squatina prima* (Winkler)
Odontaspis cf. *macrota* (Ag.)	*Physodon* sp.

FAUNA OF THE LONDON CLAY

A, B, refer to the divisions so marked in the description of the Section. Species without such a prefix were not collected *in situ*.

Actinozoa

A. *Graphularia wetherelli* M. Edw. & H.

Annelida

Serpula bognoriensis (Mant.)

A. *S. mellevillei* Nyst & Le Hon [= *heptagona* J. de C. Sby., 1844, *non* Münst., 1835]. The characteristic opercula were found.

Brachiopoda

A. *Discinisca* sp.—see Muir-Wood, 1939: 154.

Lamellibranchia

A. *Anomia scabrosa* Wood

A. *Ostrea*, a large heavy-shelled species like *O. gigantica* Sol. from Barton.

A. *Pinna affinis* J. Sby., reaching a great size and bulk, up to 9 in. long by 6 in. wide and observed in tabular septaria with its axis vertical and gaping end uppermost. The thick, prismatic, outer layer of the test was sometimes preserved over the nacreous inner coat, which usually is all that remains of this mollusc. Mr. A. G. Davis found an umbo of this *Pinna* containing several indubitable pearls: the specimen is preserved in the Geological Department, British Museum (Nat. Hist.), L.51117.

A. *Modiolus tubicola* (Wood)—in *Teredo* borings.
B. '*Pecten*' *corneus* J. Sby. [*corneolus* Wood]
B. *Glycymeris brevirostris* (J. de C. Sby.)
B. *Cyprina planata* J. de C. Sby.
A & B. *Pitaria tenuistriata* (J. de C. Sby. *non* Lam.)
A. *Abra splendens* (J. de C. Sby.)
B. *Pholadomya dixoni* J. de C. Sby.
A & B. *P. margaritacea* (J. Sby.)
B. *P. virgulosa* J. de C. Sby.
A & B. *Panopea intermedia* (J. Sby.)
B. *Cultellus affinis* (J. Sby.)
A. *Corbula globosa* J. Sby. [*wetherelli* Edw. MS.]
A. *Teredina personata* (Lam.), boring radially to the centre of a log of wood—see Wrigley, 1939: 418.
A. Well-preserved faecal pellets on septarian surfaces.

SCAPHOPODA

? *Siphonodentalium* sp.

GASTROPODA

Euspira glaucinoides (J. Sby.)
Sigatica hantoniensis (Pilk.)
B. *Turritella* aff. *terebellata* Lam.
Orthochetus elongatus Wrig.
A. *Tibia sublucida* (Edw.)
Aporrhais sowerbii (Mant.)
A & B. *Ficus londini* Wrig.
A. *F. smithii* (J. de C. Sby.)
Several specimens of the same size show that the distinction between these two species is well founded. Some examples of *F. smithii* attain the great size of 5 in. by 3½ in. diameter.
B. *Galeodea gallica* Wrig.
B. '*Cassis*' *striata* J. Sby.
B. *Murex subcristatus* d'Orb.
A. *Pollia londini* (Wrig.)
A. *P.* sp., longer than *P. londini*
B. *Streptolathyrus cymatodis* (Edw.)
Euthriofusus transversarius Wrig.
A. *E. crebrilineus* Wrig.
B. *Surculites errans* (Sol.) [*bifaciatus* J. Sby.]
A. *Bonellitia subevulsa* (d'Orb.)

A. *Bathytoma* sp. between *B. granata* (Edw.) and *B. parilis* (Edw.)
A. *Turricula cochlis* (Edw.)
A. *T. crassa* (Edw.)
A. *T. stena* (Edw.)
Ancistrosyrinx gyrata (Edw.)
Eopleurotoma wetherellii (Edw.)

CEPHALOPODA

A. *Nautilus imperialis* J. Sby.

STRATIGRAPHICAL DISCUSSION

The occurrence of the base of the Bagshot Sands above the top of the London Clay at Lower Swanwick brickyard, described above, accords with the Old Series Geological Survey map (sheet 11) of 1858, by W. H. Bristow. The New Series map, sheet 316, colour-printed in 1905, indicates Reading Beds at this spot: this must be an error, for below their supposed outcrop fossiliferous London Clay is now plainly visible.

The Lower Swanwick exposure is naturally to be compared with the sections formerly seen during the construction of the railway from Bursledon to Fareham and particularly with the London Clay of a cutting 4 miles west of the brickyard. These railway exposures were described by Elwes (1888, 1890), whose account and diagram were presented in an improved form by Osborne White (1913: 47–52). The Geologists' Association, guided by W. Whitaker, visited the railway during its construction (Whitaker, 1887: 138) and there is no reason for doubting Elwes's description of the London Clay between Fareham station and the Meon river. Unhappily, Elwes did not give the thickness of the strata he records and there is a discrepancy between the lengths of the Ordnance maps and those shown on Elwes's scale diagrams. It is clear, however, that the base of the London Clay occurs near Fareham station, whence the long cuttings westward show successive beds dipping down to the west until the junction of the London Clay and Bagshot Sands occurs at the level of the railway line on the west side of the Meon valley. Farther west, Whitaker (1902: 10) records the presence of a London Clay Basement-bed close to Swanwick station, while 1¼ miles west of that place the top of the London Clay is now seen in Lower Swanwick brickyard. It seems that the whole thickness of the London Clay is twice exposed just above or below the level of the railway line between Fareham station and Bursledon bridge, with an anticline at Swanwick station and a syncline on the western side of the Meon valley. These undulations are quite credible by their proximity to the major anticline of Portsdown.

The Elwes collection is preserved in the Museum of the Yorkshire Philosophical Society. By favour of its Curator, Mr. R. Wagstaffe, and with the kind help of Mr. G. F. Elliott, it has been possible to examine Elwes's Fareham fossils in London. They most decidedly confirm the conclusion that the Lower Swanwick strata are not represented in the Fareham railway section. Generally, Elwes's material shows that his published list may be received with confidence, but, apart from any mere revision of generic names, the following corrections may be noted, Elwes's determinations being within brackets:

[*Leda substriata* ? Mor.] = *Nuculana oblata* (S. Wood)
[*Ostrea flabellula* Lam.] = *Ostrea multicostata* Desh.
[*Astarte tenera* Sby.] = *Astarte subrugata* S. Wood
[*Turritella imbricataria* Lam.] = *Turritella* aff. *dixoni* Desh.
[*Rostellaria lucida* Sby.] = *Tibia sublucida* (Edw.)
[*Natica labellata* Lam.] = *Euspira glaucinoides* (J. Sby.)
[*Cassidaria nodosa* Sol.] = *Galeodea gallica* Wrig.
[*Pisania sublamellosa* Desh.] = *Pseudoneptunea curta* (J. Sby.)
[*P. morrisi* Edw.] = *Pollia* aff. *londini* (Wrig.)
[*Cancellaria laeviuscula* Sby.] = *Bonellitia subevulsa* (d'Orb.)
[*Pleurotoma* near *wetherelli* Edw.] = *Eopleurotoma simillima* var. *crassilinea* (Edw.)

Two unrecorded species have been found in this material—*Eopleurotoma koninckii* (Edw. *non* Nyst) and *Bullinella* aff. *uniplicata* (J. de C. Sby.). The remarkable feature of this collection is the presence of no fewer than five well-defined species, not merely undescribed but which, so far as I know, have not yet been found in the London Clay of any other locality. They comprise *Arca*, *Sconsia* (a genus new to the London Clay), *Murex* 2 spp., and *Siphonalia*.

A fair idea of the succession of London Clay strata in this locality will be obtained by following Elwes's account from the base at Fareham station upwards to the stiff, blue clay immediately above the two pebble-beds with *Terebratula*, allowing for a probable gap in the record by the interruption of the section at the Meon valley and completing it by the strata seen in Lower Swanwick brickyard here described up to the Bagshot Sands. The total thickness, by analogy with the complete London Clay found in borings at Woolston and at Southampton Common, appears to be about 300 ft. [Whitaker (1887: 138) noted that the Fareham *Terebratula* occurred 'in nests like miniature mussel-banks'. Muir-Wood (1933: 170) has described *Terebratula hantonensis* from the Fareham railway-cutting.]

In comparing the fossil mollusca of the brickyard with those recorded from Fareham, one notices that although many of the gastropoda found in the brickyard occur in the *Terebratula*-bed of the railway and in the sandy clay below it, i.e. beds 2 and 3 of the version by Osborne White (1913: 48), yet there are differences between the two faunas which become significant by the proximity of the sections. The flabelliform *Ostrea*, the *Turritella* of *imbricataria* type, and the *Ditrupa* which was found in masses at several horizons on the railway are conspicuously absent in the brickyard where, also, there is no trace of a *Terebratula*-bed or of the *Dentalium* which occurred commonly in the sands below it. '*Pecten*' *corneus* and two very distinct species of *Pholadomya* are peculiar to the brickyard and are quite common there. Bed A, so notable at Lower Swanwick, with its huge *Pinna*, *Ostrea*, and *Ficus smithii*, is quite different from anything recorded by Elwes.

The comparison of sections of London Clay in the Hampshire basin is a most difficult task. Bognor, Portsmouth, Southampton, Fareham, Whitecliff Bay, and

Alum Bay offer satisfactory records of a complete London Clay, deposited in a shallow sea and presenting the utmost variety and discrepancy, which, at present, defy fruitful correlation.

During the recent war this brickyard was unworked and the section recorded above has become totally obscured by talus and vegetation. Recently, work has been resumed by a new method of excavating clay below the lowest horizon (A) of the earlier workings. Many fossils are to be found and it is hoped that the collection and study of them will fill the gap in a complete, local London Clay sequence noted above to be found in the railway section at the Meon valley.

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